

TRAPLINERS IN THE TREES: HUMMINGBIRD POLLINATION OF *ERYTHRINA* SECT. *ERYTHRINA* (LEGUMINOSAE: PAPILIONOIDEAE)¹

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ABSTRACT

Erythrina sect. *Erythrina* comprises 36 species of hummingbird-pollinated trees and shrubs, distributed principally in Mesoamerica. Avian floral visitors—including nectar thieves as well as pollinators—were observed at 17 populations of 13 species in southern Mexico and Costa Rica. Legitimate pollinators were all “high-reward traplining” hummingbirds with long bills and non-territorial foraging behavior, including in particular two species of *Heliomaster*. Nectar thieves included a variety of short-billed hummingbirds and passerine birds. Measurements of nectar volume, sugar concentration, and flowering behavior indicate that the caloric value of nectar in open flowers produced by one tree per day is insufficient to support a single hummingbird’s energetic requirements; therefore, territorial defense by a hummingbird of a single tree is precluded. The traplining hummingbirds appear to be effective agents of pollen flow among conspecific trees in the typically low-density *Erythrina* populations. The pollination system of sect. *Erythrina* is a canopy-level analogue of the high-reward traplining systems involving hermit hummingbirds and understory plants such as *Heliconia* (Musaceae).

Erythrina L. (Leguminosae: Papilionoideae) comprises about 112 species distributed throughout the tropical regions of the world and extending into warm temperate areas in both the northern and southern hemispheres (Krukoff & Barneby, 1974; Neill, in press). Most species are trees or shrubs, but about 10 species occurring in climates with pronounced dry and/or cool seasons are perennial herbs with large, woody rootstocks. *Erythrina* species occur in a very wide variety of habitats, from lowland tropical rain forests to very arid subtropical deserts to highland coniferous forests above 2,500 m in elevation.

Erythrina species have red or orange flowers and copious nectar and are adapted to pollination by nectarivorous birds. Two distinct syndromes of ornithophily are evident. All 42 of the Old World species and 15 of the 70 New World species are pollinated by “perching birds” of several families in the order Passeriformes. Passerine birds cannot hover efficiently or for any length

of time, and the inflorescences of passerine-pollinated *Erythrina* are oriented in such a way that the birds can perch while feeding on nectar from the flowers. The corolla standard is usually broad and the flowers are open, with exposed reproductive parts. Pollen is deposited on the feeding bird’s breast (Cruden & Toledo, 1977). In contrast, 55 of the New World species of *Erythrina* (nearly half the genus) are pollinated by hummingbirds (Trochilidae), which occur only in the New World. Hummingbirds are the most specialized of nectarivorous birds and are the only ones that hover while feeding. The corolla standard of hummingbird-pollinated *Erythrina* is narrow and conduplicately folded to form a “pseudotube,” concealing the wing and keel petals as well as the reproductive parts. The flower resembles the tubular corollas of many gamopetalous hummingbird-pollinated plants, but in *Erythrina* the pseudotube is not sealed on the ventral side where the margins of the corolla standard meet. The inflorescence axis of the humming-

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bird-pollinated species is erect and the flowers are oriented outward, providing no perch for the hovering hummingbirds.

The American hummingbird-pollinated species are included in six different sections of subg. *Erythrina*; these I believe to have been derived from passerine-pollinated groups by convergent evolution in several independent lineages. The largest by far of the hummingbird-pollinated groups is sect. *Erythrina* (36 species) with its center of diversity in northern Central America and southern Mexico (Neill, in press). Most species of sect. *Erythrina* are canopy or subcanopy trees, ranging in height from 5 m in semiarid scrub to 25 m or more in lowland rain forest or cloud forest. A few species inhabit the understory and light gaps of wet forests. Many have restricted ranges and are edaphic specialists; an example is *E. tuxtlana*, which grows only on limestone outcrops in lowland wet forests in southeastern Mexico.

A number of field studies of pollination in *Erythrina* have been conducted in recent years, including observations of passerine-pollinated as well as hummingbird-pollinated species (Toledo, 1974; Toledo & Hernández, 1979; Hernández & Toledo, 1979, 1982; Cruden & Toledo, 1977; Feinsinger et al., 1979; Morton, 1979; Steiner, 1979; Guillarmod et al., 1979). An extensive survey of hummingbird pollination of *Erythrina* tree species, however, was lacking prior to the research reported here.

HUMMINGBIRD FORAGING BEHAVIOR: A REVIEW

Hummingbird species differ in size, bill morphology, and foraging behavior as do the floral morphology and flowering patterns of the plant species they visit (Feinsinger & Colwell, 1978). The two principal behavioral types are territorialists, which feed at large patches of flowers, defending the flowers against usurpers; and trapliners, which do not defend territories but rather visit small, widely spaced clumps of flowers on repeated foraging circuits. The latter may be further subdivided into "low-reward" trapliners, relatively small, short-billed birds, and "high-reward" trapliners, birds with relatively large bodies, high energetic requirements, and long or curved bills. High-reward trapliners are the most "specialized" of hummingbirds in the sense that they have the highest fidelity to particular plant species. These are the only birds capable of pol-

linating plants with long-tubular flowers, and they provide effective cross-pollination service to plant species with low population densities. The most well-studied of the high-reward trapliners are the hermit hummingbirds (Phaethorninae), which forage principally in lowland and mid-elevation wet forest understories on widely spaced, nectar-rich herbs and shrubs.

Stiles (1978, 1981) noted that very few hummingbird-pollinated plants are canopy trees; in contrast, many ornithophilous plants of the Old World, pollinated by passerine birds, are trees. Stiles reasoned that this difference is related to the social systems of the two bird groups. Passerine nectarivores generally forage in large flocks, whereas hummingbirds are virtually always solitary. A large concentration of flowers on a large tree would be parceled up into feeding territories by hummingbirds, thus drastically reducing cross-pollination. A large flock of passerine birds, in contrast, could quickly exhaust the resources of even a large tree, and the flock would be compelled to move on to the next tree, thus effecting cross-pollination.

Erythrina is an exception to the general paucity of hummingbird-pollinated canopy or subcanopy trees. It should be instructive to determine by observations in the field whether Stiles's prediction holds true for hummingbird-pollinated *Erythrina*. If hummingbirds parcel the crown of a tree into several feeding territories, they may reduce intertree pollen flow; alternatively, hummingbird-pollinated *Erythrina* trees may possess adaptations that reduce territorial behavior and promote intertree movement of the hummingbird pollen vectors.

In the present study of hummingbird pollination in natural populations of trees of sect. *Erythrina*, several questions were addressed: Do the hummingbirds that pollinate *Erythrina* behave as territorialists or as trapliners? How specialized are *Erythrina* pollinators? Another goal was to assess the potential for pollen transfer between different species of *Erythrina*. Experimental hybridization studies (Neill, in press) indicate that species of sect. *Erythrina* are highly interfertile, but unless the hummingbird pollen vectors carry pollen from one species to another, hybridization will not take place under natural conditions. This assessment required information about the flight and foraging patterns of the birds, and whether the *Erythrina* species shared the same pollinators or had different, host-specific pollinators.

MATERIALS AND METHODS

FLORAL BIOLOGY AND BREEDING SYSTEMS

Observations on phenology and other details of *Erythrina* floral biology, as well as experimental studies of genetic self-incompatibility, were made on wild populations in Mesoamerica and on cultivated trees in Hawaii. The experimental methods for the breeding system studies are described by Neill (in press).

OBSERVATIONS OF FLORAL VISITORS

Floral visitors to 17 populations of 13 species of hummingbird-pollinated *Erythrina* trees were observed in Mesoamerica. These included four wet season-flowering species in Costa Rica, July–September 1981, and nine dry season-flowering species in southern Mexico, January–April 1983. All but one of the species is in sect. *Erythrina*; the exception is *E. gibbosa* from Costa Rica, in the monotypic sect. *Gibbosae*. Flowering and pollination patterns in this species are very similar to those in sect. *Erythrina*.

For the 13 species a total of 195 person-hours of observation was conducted. For a population the number of observation hours ranged from 2.5 to 45.5. Most of the observations were made between dawn and 12 P.M., because floral visitor activity is usually greater in the early morning and drops substantially by noon. Some observations were conducted in the late afternoon when avian floral visitors typically become more active after the midday lull.

At the beginning of each observation day I counted the number of open flowers on each tree. For each bird visit to a tree crown, I recorded the time, duration of visit, number of flowers probed, and direction of arrival and departure. I judged qualitatively the frequency of the visitor's contact with the reproductive parts of the flower, as a measure of potential pollination efficacy. Many of the non-pollinating passerine bird visitors actually destroyed or removed a considerable number of flowers daily, reducing the number available to subsequent visitors to the tree. This activity was recorded and entered into the daily flower censuses.

NECTAR PRODUCTION

I sampled daily nectar production in four species in sect. *Erythrina*: *E. globocalyx* and *E.*

costaricensis inhabiting wet forests in Costa Rica, and *E. chiapasana* and *E. goldmanii* in dry forests of Chiapas, Mexico. Because the inflorescences in the tree crowns were difficult to reach from the ground, repeated sampling of nectar secretion of individual flowers over the course of a day was not possible; only a day's total production was sampled.

In the late afternoon, flowers due to open the following day were bagged with mosquito netting. These "first-day" flowers were removed at about 4 P.M. the following day, and nectar volume from each flower was measured by repeated probing with a 10- or 25-ml calibrated micro-pipette.

Nectar production for "second-day" flowers of *E. goldmanii* and *E. chiapasana* was estimated in the following manner: inflorescences were bagged with mosquito netting in the late afternoon as for first-day flowers, and nectar was allowed to accumulate in the isolated flowers for two days. Total nectar accumulation was measured at 4 P.M. on the second day. The mean first-day accumulation of nectar subtracted from the mean 2-day accumulation yields the estimated second-day nectar production. (This method assumes that nectar removal does not influence secretion.) All bagged flowers fell off by the morning of the third day.

Sugar concentration expressed as percent sucrose equivalence (Bolten et al., 1980) was measured for each flower or for the pooled nectar of several flowers using an American Optical model 10431 temperature-compensated hand refractometer. With the figures for nectar volume and sugar content, the mean caloric value of the nectar per flower was calculated for each population sampled.

RESULTS

FLORAL BIOLOGY AND BREEDING SYSTEMS

In most passerine-pollinated species of *Erythrina* the stamens and stigma are well separated at anthesis and the flowers are homogamous, i.e., pollen is released from the anthers and the stigma becomes receptive simultaneously on the first day of flowering. In sect. *Erythrina* and the other hummingbird-pollinated sections of the genus, in contrast, the stamens and stigma are held in close proximity, tightly enclosed in the floral pseudotube, and the flowers are protandrous.

On the first day of anthesis the staminal fila-

TABLE 1. Observations of avian floral visitors to *Erythrina* tree species.

| Species | Locality ¹ | Trees ² | Hours ³ | Pollinators | Nectar Thieves & Robbers | |
|---|--|--------------------|--------------------|--|---|---|
| | | | | | Hummingbirds | Passerines |
| 1. <i>E. americana</i> | Mexico: Oaxaca Coatlán | 4 | 9 | <i>Heliomaster constantii</i> | — | <i>Icterus galbula</i> |
| 2. <i>E. berte-roana</i> × <i>E. folkersii</i> | Mexico: Chiapas Palenque | 5 | 3.5 | <i>Anthracothorax prevostii</i> | <i>Anthracothorax prevostii</i> | <i>Icterus maculialatus</i> <i>Pheucticus ludovicianus</i> |
| 3. <i>E. berenices</i> | Mexico: Veracruz Tequila | 2 | 2 | <i>Eugenes fulgens</i> | — | — |
| 4. <i>E. chiapana</i> | Mexico: Chiapas El Sumidero | 8 | 15.5 | <i>Heliomaster constantii</i> | — | <i>Icterus wagleri</i> |
| 5. <i>E. chiapana</i> | Mexico: Chiapas Teopisca | 6 | 18 | <i>Eugenes fulgens</i> | <i>Hylocharis leucotis</i> | <i>Diglossa baritula</i> <i>Icterus galbula</i> |
| 6. <i>E. cochleata</i> | Costa Rica: Heredia La Selva | 6 | 20 | <i>Heliomaster longirostris</i> | <i>Chalybura urochrysia</i> | — |
| 7. <i>E. costaricensis</i> | Costa Rica: Puntarenas San Vito de Java | 1 | 5 | <i>Heliomaster longirostris</i> | <i>Phaeochroa cuvierii</i> | — |
| 8. <i>E. gibbosa</i> | Costa Rica: Alajuela Monteverde | 2 | 11 | <i>Phaethornis guy</i> | <i>Lampornis hemileucus</i> | — |
| 9. <i>E. globocalyx</i> | Costa Rica: San Jose Las Nubes | 5 | 8.5 | <i>Eugenes fulgens</i> <i>Campylopterus hemileucurus</i> | — | — |
| 10. <i>E. goldmanii</i> | Mexico: Chiapas El Sumidero | 12 | 45.5 | <i>Heliomaster constantii</i> | — | <i>Icterus gularis</i> <i>I. pectoralis</i> <i>I. wagleri</i> |
| 11. <i>E. folkersii</i> | Mexico: Veracruz Los Tuxtlas | 2 | 3.5 | <i>Phaethornis superciliosus</i> <i>Campylopterus hemileucurus</i> <i>C. curvipennis</i> | — | — |
| 12. <i>E. folkersii</i> | Mexico: Chiapas Palenque | 2 | 4.5 | <i>Phaethornis superciliosus</i> | <i>Amazilia tzacatl</i> | <i>Icterus galbula</i> <i>I. prosthemelas</i> |
| 13. <i>E. lanata</i> | Mexico: Oaxaca Puerto Escondido | 2 | 4.5 | <i>Heliomaster constantii</i> | — | — |
| 14. <i>E. lanata</i> | Mexico: Jalisco Chamela | 2 | 7.0 | <i>Heliomaster constantii</i> | — | <i>Cassiculus melanicterus</i> |
| 15. <i>E. pudica</i> | Mexico: Chiapas El Aguacero | 8 | 16.0 | <i>Heliomaster constantii</i> | — | <i>Icterus gularis</i> |
| 16. <i>E. tuxtlana</i> | Mexico: Chiapas Malpaso | 3 | 15.0 | <i>Heliomaster constantii</i> <i>Anthracothorax prevostii</i> | <i>Amazilia cyanocephala</i> <i>A. tzacatl</i> | <i>Coereba flaveola</i> <i>Cyanerpes lucidus</i> <i>Icterus graduacauda</i> |

TABLE 1. Continued.

| Species | Locality ¹ | Trees ² | Hours ³ | Pollinators | Nectar Thieves & Robbers | |
|------------------------|------------------------------|--------------------|--------------------|----------------------------------|--------------------------|--------------------------------|
| | | | | | Humming-birds | Passerines |
| | | | | <i>Eugenes fulgens</i> | | <i>Pheucticus ludovicianus</i> |
| 17. <i>E. tuxtlana</i> | Mexico: Veracruz Uxpanapa | 1 | 5.5 | <i>Campylopterus curvipennis</i> | <i>Eupherusa eximia</i> | — |

¹ Complete locality and voucher data for each observation are listed in Appendix.

² Number of individual trees observed.

³ Person/hours of observation.

ments are fully grown and pollen is released from the stamens situated near the apex of the corolla within the pseudotube. At this stage the style is shorter than the stamens and the stigma is not receptive. The style and ovary continue to elongate during the night after the first day of flowering. By the second day, when most of the pollen has been removed by floral visitors, the stigma, now receptive and with a sticky exudate on its surface, is held a few mm beyond the anthers, just inside the mouth of the pseudotube at the apex of the corolla. Each flower, then, is functionally male on the first day and functionally female on the second. Unpollinated flowers usually abort after the second day but sometimes remain for a third or fourth day before aborting; the stigma appears to remain receptive during this time.

The inflorescence of sect. *Erythrina* is a pseudoraceme with fascicles of three flowers each arranged spirally on the erect rachis. Anthesis occurs sequentially from bottom to top of the inflorescence, and usually one or two fascicles of flowers open each day. An individual inflorescence, with 30–50 fascicles, blooms for two or three weeks. An inflorescence in “full bloom” is composed of three to nine functionally female flowers at the bottom (in one to three fascicles), three to six functionally male flowers in the fascicles just above the females, and above them floral buds at progressively younger developmental stages.

Inflorescence development in an individual *Erythrina* tree is staggered, so a tree often blooms for two to three months or more. Blooming among trees in a population is also staggered, so a population is often in bloom for four to five months annually or even longer. Some species remain in bloom for a shorter period, one to two months

within a population. Detailed, multi-year phenological data for any particular site, however, is not available.

Most species of sect. *Erythrina* flower during the dry season, from January to May in Mesoamerica, and are leafless when in flower. Leaves flush, in general, after flowering has ceased and while fruits are developing, prior to or just after the onset of the rainy season in May or June. Some species flower during the rainy season, June to October. These species also usually shed all their leaves before flowering and flush a new set of leaves as flowering ceases. This behavior is unusual: few other tree taxa in the Neotropics, especially in very wet forests, shed leaves during the rainier portion of the year and retain them during the drier portion.

The data presently available suggest that all *Erythrina* species are genetically self-compatible (Neill, in press). The fitness of progeny resulting from self-pollination is significantly lower than that of progeny resulting from outcrossing; outcrossing appears to be predominant in the breeding systems of *Erythrina*. Some seed set from geitonogamous pollinations and even from occasional autogamy, which probably occurs in natural populations.

FLORAL VISITORS

The avian visitors to the flowers of most observed *Erythrina* populations included hummingbird and passerine “illegitimate” visitors, which obtained nectar but did not effect pollination, as well as “legitimate” hummingbird pollinators (Table 1). Pollination records for each *Erythrina* species are summarized in Table 2, which encompasses prior reports on hummingbird-pollinated tree species: *Erythrina lanceo-*

TABLE 2. Species of hummingbirds observed as legitimate pollinators on 15 species of *Erythrina*. Abbreviations in parentheses refer to the countries in which species were observed (M = Mexico, C = Costa Rica, and T = Trinidad).

| Hummingbirds | <i>Erythrina</i> Species | | | | | | | | | | | | | | |
|-----------------------------------|--------------------------|----------------------|----------------------|--------------------------|--------------------------|-------------------------|-------------------------|-----------------------------|------------------------|-----------------------|-----------------------------|-------------------------|--------------------------|-------------------------|-----------------------|
| | <i>E. goldmanii</i> (M) | <i>E. pudica</i> (M) | <i>E. lanata</i> (M) | <i>E. lanceolata</i> (C) | <i>E. chiapasana</i> (M) | <i>E. americana</i> (M) | <i>E. cochleata</i> (C) | <i>E. costaricensis</i> (C) | <i>E. tuxtiana</i> (M) | <i>E. pallida</i> (T) | <i>E. berteriana</i> (M, C) | <i>E. berenices</i> (M) | <i>E. globocalyx</i> (C) | <i>E. folkersii</i> (M) | <i>E. gibbosa</i> (C) |
| <i>Heliomaster constantii</i> | + | + | + | + | + | + | | | | | | | | | |
| <i>H. longirostris</i> | | | | | | | + | + | + | + | + | | | | |
| <i>Eugenes fulgens</i> | | | | | + | + | | | + | | | + | + | | |
| <i>Campylopterus hemileucurus</i> | | | | | | | | | | | | + | + | + | |
| <i>C. curvipennis</i> | | | | | | | | | + | | | | | + | |
| <i>Anthracothorax prevostii</i> | | | | | | | | | + | | + | | | + | |
| <i>Phaethornis guy</i> | | | | | | | | | | | | | + | | + |
| <i>Ph. superciliosus</i> | | | | | | | | | | | | | | + | |
| <i>Glaucis hirsuta</i> | | | | | | | | | | + | | | | | |

lata in Costa Rica (P. Feinsinger, pers. comm.) and *E. pallida* in Trinidad and Tobago (Feinsinger et al., 1979).

For this discussion I have adopted a modified version of Inouye's (1980) terminology for floral larceny: "nectar robbers" make a hole or otherwise damage floral tissue to gain access to the nectar, while "nectar thieves" use the opening used by legitimate pollinators, but a mismatch of the morphologies of flower and animal precludes pollination. The distinction between nectar thieves and robbers is important because robbers may damage the ovary or styler tissue and often destroy or remove the entire flower, and thus may have a much greater effect in reducing the reproductive potential of the plant than do nectar thieves.

Bill lengths (obtained primarily from Ridgway, 1911) of the hummingbird species observed as pollinators and illegitimate visitors to *Erythrina* trees are compared in Figure 1. Legitimate pollinators all have bills longer than 28 mm, whereas nectar thieves and robbers, with one exception, have bills shorter than 22 mm.

POLLINATORS

Nine species of hummingbird were observed as legitimate pollinators of the 15 species of *Er-*

ythrina trees. All of the hummingbird pollinators may be characterized as long-billed, high-reward trapliners, although some behaved as territorialists or even nectar thieves on certain occasions, as detailed below.

I observed two species of hermit hummingbirds (Phaethorninae) pollinating *Erythrina*: *Phaethornis guy* and *P. superciliosus*. A third hermit species, *Glaucis hirsuta*, was reported as a pollinator of *E. pallida* in Trinidad by Feinsinger et al. (1979). The hermits visited principally the smaller understory species of *Erythrina* but rarely were in the forest canopy. Their foraging behavior at understory *Erythrina* is similar to that documented for understory herbs such as *Heliconia* (Stiles, 1975) or shrubs such as *Apheleandra* (McDade, 1984).

The remaining six *Erythrina* pollinators are non-hermits (Trochilinae); all are long-billed, high-reward trapliners which forage like hermits, but usually in the forest canopy or open areas rather than in the understory. *Heliomaster constantii* is the principal or sole known pollinator of at least six *Erythrina* species in the dry forests on the Pacific slope of Mesoamerica. Its congener *H. longirostris* has been reported from four *Erythrina* species in more humid lowland forests on both the Pacific and Caribbean slopes of Me-

ERYTHRINA FLORAL VISITORS: HUMMINGBIRDS

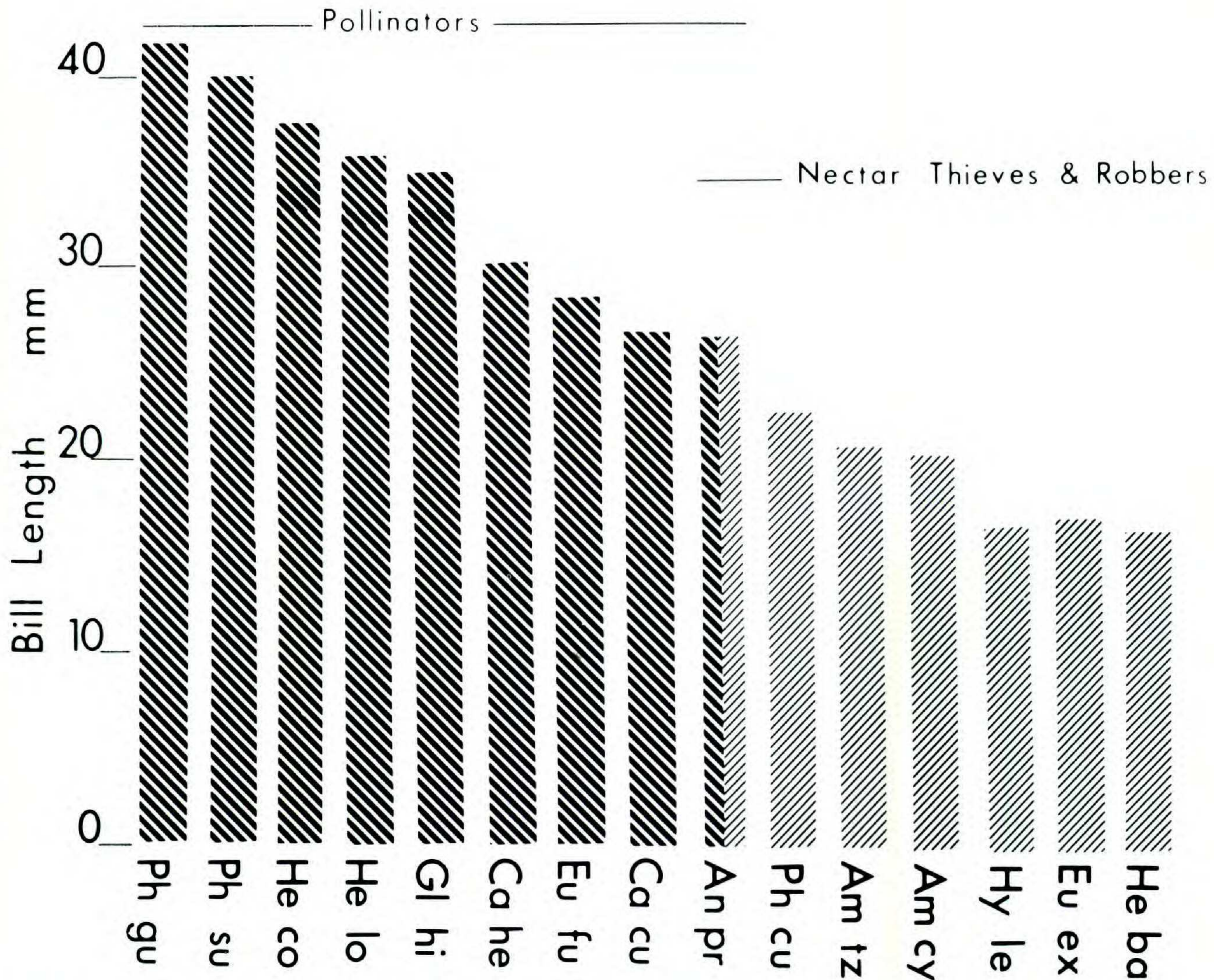


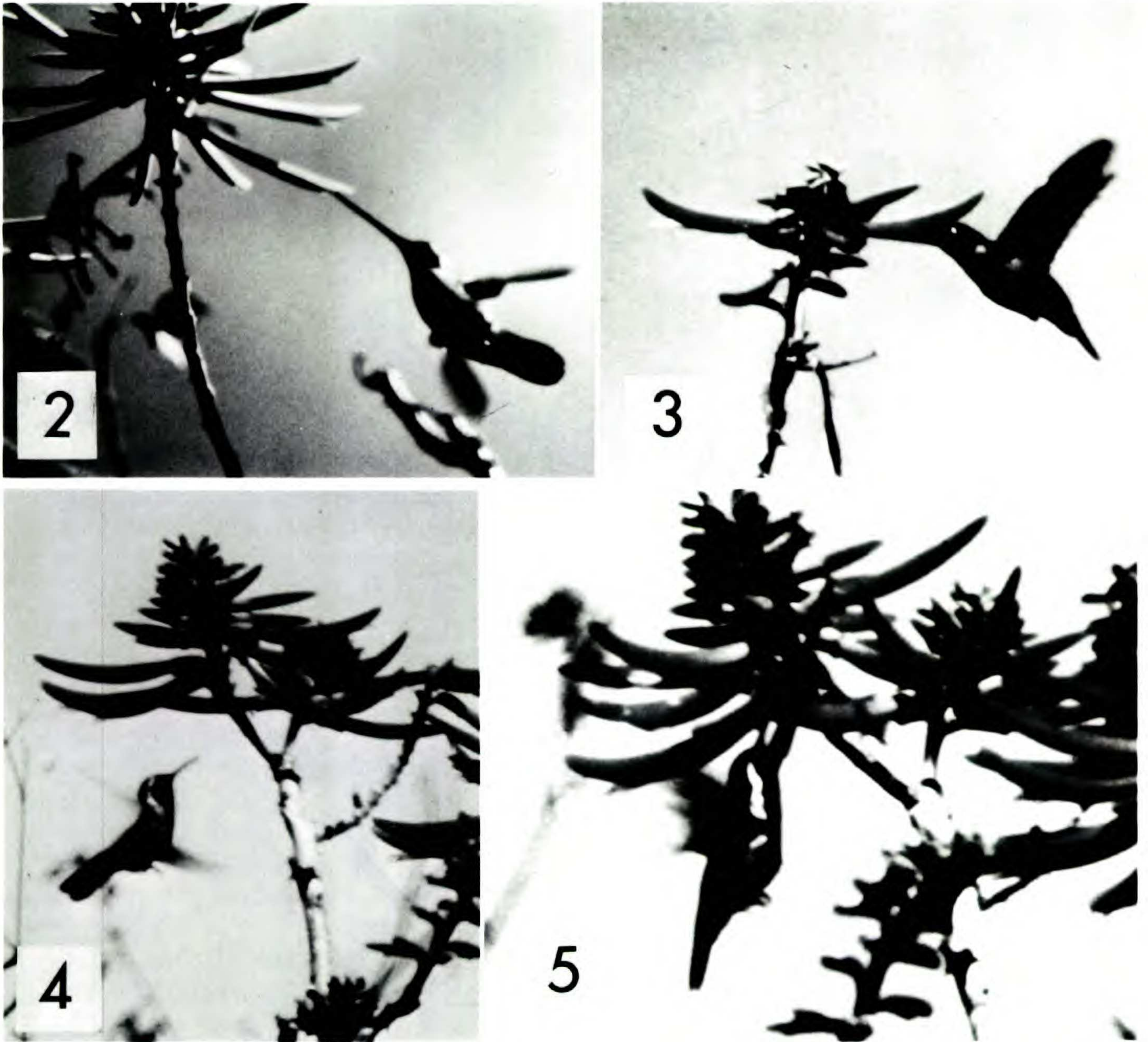
FIGURE 1. Bill lengths of hummingbird visitors to *Erythrina* trees, including pollinators and illegitimate visitors. Ph gu = *Phaethornis guy*; Ph su = *Phaethornis superciliosus*; He co = *Heliomaster constantii*; He lo = *Heliomaster longirostris*; Gl hi = *Glaucis hirsuta*; Ca he = *Campylopterus hemileucurus*; Eu fu = *Eugenes fulgens*; Ca cu = *Campylopterus curvipennis*; An pr = *Anthracothorax prevostii*; Ph cu = *Phaeochroa cuvierii*; Am tz = *Amazilia tzacatl*; Am cy = *Amazilia cyanocephala*; Hy le = *Hylocharis leucotis*; Eu ex = *Eupherusa eximia*; He ba = *Heliiothryx barroti*.

soamerica, and from *E. pallida* in Trinidad (Feinsinger et al., 1979). *Eugenes fulgens* is found mostly in the highlands of Mesoamerica above 1,500 m. It is the principal pollinator of at least four highland species of *Erythrina*, and I also observed it below 1,000 m pollinating *E. tuxtana* in southern Mexico. *Campylopterus hemileucurus* is a bird of wet forests from near sea level to 1,800 m and has been observed pollinating three *Erythrina* species in such habitats. *Campylopterus curvipennis* was observed as a pollinator of two *Erythrina* species in low- to mid-elevation wet forests of southern Mexico.

Anthracothorax prevostii was the least consistent *Erythrina* pollinator. This bird of low- to

mid-elevation humid forests sometimes behaved as a legitimate pollinator and contacted the reproductive parts of *Erythrina* like the other long-billed trapliners. More frequently, however, *Anthracothorax* was a nectar thief, as described below.

The species of hummingbirds that pollinate sect. *Erythrina* all behave in a similar manner when feeding at the flowers. The hummingbird first approaches the inflorescence and hovers to align its bill precisely with the axis of the first flower it is to visit (Fig. 2). It inserts its bill at the apex of the flower; at full penetration the reproductive parts of the flower always contact the bird's throat, upper chest, or the base of the



FIGURES 2-5. Hummingbird pollinators and nectar thieves of *Erythrina* sect. *Erythrina*.—2. Pollinator *Heliomaster constantii* positioning self to feed at flowers of *E. lanata*; dry forest near the Pacific coast, Pochutla, Oaxaca, Mexico. Bill is inserted at apex of corolla.—3. *Eugenes fulgens* pollinating *E. chiapasana*; highland pine-oak forest, Teopisca, Chiapas, Mexico. At full insertion of the bill, pollen is deposited at base of bill or on upper throat.—4-5. *Hylocharis leucotis*, a short-billed nectar thief, approaching and foraging at flowers of *E. chiapasana*; same locality as in Figure 3. The bill is inserted into the mouth of the calyx or the slit of the corolla "pseudotube" to obtain nectar; reproductive parts of the flower are not contacted.

bill (Fig. 3). The bird remains hovering at this position for up to five seconds, then withdraws and moves to another flower in the inflorescence or to another inflorescence.

The pollination records summarized in Table 2 indicate that there is no species-specific, one-to-one relationship of *Erythrina* species and hummingbird species. The ecological and geographic distribution of any single *Erythrina* species does not correspond precisely with that of any pollinator species. Most of the hummingbirds have been observed at several species of

Erythrina at different localities in the birds' range, and more than one pollinator has been recorded for many of the *Erythrina* species. The bird species are quite similar to one another behaviorally and morphologically, and the tree species are also quite similar to one another in terms of floral morphology, flowering behavior, and nectar rewards (the last is discussed below). *Erythrina* sect. *Erythrina* and related groups are evidently adapted to pollination by the high-reward trapliner guild of hummingbirds as a whole. This, however, is a small subset of all hummingbirds.

In Mesoamerica, there are very few additional hummingbird species with the appropriate morphology and behavior for *Erythrina* tree pollination, other than the nine species listed in Table 2. (*Doryfera ludoviciae* in the highlands of Costa Rica and Panama may be the only high-reward trapliner in the region not reported as an *Erythrina* pollinator [P. Feinsinger, pers. comm.])

On the local community level, often only a single high-reward traplining hummingbird is present so that many populations of *Erythrina* are pollinated by a single bird species. In the lowland dry forests of Pacific Mesoamerica, *Heliomaster constantii* is the only appropriate hummingbird present, so it is undoubtedly the sole pollinator of the *Erythrina* tree species restricted to Pacific dry forests.

The hummingbirds are not strict specialists on *Erythrina*. Well-studied species such as *Eugenes fulgens* have been reported visiting a number of other plant species. The two *Heliomaster* species may be more specialized as *Erythrina* foragers than are the other hummingbird genera. During the course of his extensive community-level studies of hummingbirds, P. Feinsinger (pers. comm.) observed *Heliomaster longirostris* on Trinidad to feed only at *Erythrina pallida* and at the apocynaceous vine *Mandevilla hirsuta*; while at Monteverde, Costa Rica, *Heliomaster constantii* visited exclusively different species of the same two plant genera.

NECTAR THIEVES

The nectar thieves of *Erythrina* sect. *Erythrina* are primarily short-billed, small-bodied, generalist hummingbirds. Observed nectar thieves include several species of *Amazilia*, *Hylocharis leucotis*, *Eupherusa eximia*, and *Chalybura urochrysis* (Table 1). The short bills of these birds preclude them from reaching the floral nectar by inserting their bills at the apex of the corolla. Nectar thieves take advantage of the incompletely sealed tube of the *Erythrina* corolla. They approach the flower from below (Fig. 4) and, often with some struggle and manipulation of their bills and bodies, slip their bills into the proximal end of the ventral slit of the pseudotube formed by the corolla standard, or into the mouth of the calyx (Fig. 5). They are thus able to gain access to the nectar within the pseudotube without damaging reproductive tissue. Nectar thief activity is concentrated at the base of the corolla, and thieves were never observed to contact the

reproductive parts of the flowers at the apex of the corolla. Unlike the pollinators, thieves frequently grasp the flowers with their feet when feeding and clamber over the inflorescence to reach adjacent flowers. They may damage the surface of the corolla somewhat, but they do not appear to damage the ovary itself. Small nectar thieves may lack the power to pierce the thick *Erythrina* perianth as do the larger-bodied nectar robbers.

Most of the hummingbird nectar thieves are small species with bills under 21 mm long and bodies weighing less than 6 g. An exception is *Anthracothorax prevostii*, whose bill length of 28 mm is within the low end of the range of the legitimate pollinators and whose body size of 10 g is equivalent to that of the pollinators. *A. prevostii* was occasionally seen visiting *Erythrina* flowers in the manner of a true pollinator, but more often it behaved as a nectar thief in a manner similar to the smaller opportunistic birds.

NECTAR ROBBERS: HUMMINGBIRDS

Nectar-robbing hummingbirds have shorter bills than the pollinators but are larger in body size and more powerful than the nectar thieves. The robbers pierce the calyx or base of the corolla with their needle-like bills to gain access to *Erythrina* nectar.

I observed the large (12 g) hummingbird *Phaeochroa cuvierii* repeatedly robbing flowers of a roadside *Erythrina costaricensis* near San Vito de Java in southern Costa Rica. Hovering beneath or beside the inflorescence, the bird placed the tip of its bill against the fleshy calyx and with three or four sharp thrusts punctured through the calyx to plunder the nectar. Usually the robber hovered while piercing the flower, but sometimes it perched on the inflorescence. Flowers strewn on the ground below the tree had up to six puncture holes through the underside of the calyx, indicating that *Phaeochroa* returned to a single flower several times to drain it of nectar. Most pierced flowers were soon aborted, and some had signs of damage to the ovary caused by the robber's bill. On two successive mornings, a *Phaeochroa* repeatedly robbed an *E. costaricensis* tree that was also visited at intervals by a legitimate pollinator, *Heliomaster longirostris*. When on occasion the two birds arrived to feed at the tree simultaneously, a territorial fight ensued.

In the same region of southern Costa Rica

where I made the foregoing observations of *E. costaricensis*, Skutch (1971) reported that *Heliomaster longirostris* pollinated the flowers of *Erythrina berteriana* while *Phaeochroa cuvierii* and another short-billed hummer, *Heliostyris barrotii*, robbed them by piercing the calyx. *Erythrina costaricensis* flowers during the Mesoamerican rainy season, August–November, while *E. berteriana* flowers during the dry season, late December to March. The similarity of visitation patterns reported for these two species with different flowering phenologies in the same region (they are not strictly sympatric) suggests that together they support the same pollinators and illegitimate visitors in succession for a considerable portion of the year.

NECTAR ROBBERS: PASSERINE BIRDS AND PARROTS

All of the non-hummingbird visitors to *Erythrina* sect. *Erythrina* are nectar robbers and generally destroy the reproductive potential of the flowers they visit. These robbers include passerine birds in the families Icteridae, Coerebidae, and Fringillidae, and the non-passerine parrot family Psittacidae. Icterids and coerebids are legitimate pollinators of some *Erythrina* species in the Neotropics, but on sect. *Erythrina* they are strictly parasitic.

I observed seven species of orioles (*Icterus* spp.) robbing eight species of *Erythrina* in Mexico and the icterid *Cassiculus melanicterus* robbing one *Erythrina* species. Orioles were the most frequently observed of all robbers and exhibited the most complex behavior to obtain the nectar. Typically, an oriole would pluck a flower with its bill, then hold it against a branch with one foot and jab its bill into the mouth of the calyx to reach the nectar. After plundering the flower, the oriole would drop it and pluck another. The calyx was split open in this process, and the ground beneath a tree preyed upon by orioles would typically be littered with split flowers. This allowed me to count the number of flowers consumed daily by the orioles. Sometimes an oriole would impale a flower on a thorn of an *Erythrina* tree branch to hold it in place while the oriole imbibed the nectar; the impaled flowers were left hanging on the branch.

Oriole species vary in their degree of specialization as nectar feeders (Stiles, 1981). Some evidently obtain a high proportion of their caloric requirements from floral nectar, at least during certain seasons of the year. Orioles are important

legitimate pollinators of some *Erythrina* species such as the widespread *E. fusca* (sect. *Duchassaingia*) (Morton, 1979) and the central Mexican endemic *E. oliviae* (sect. *Olivianae*) (Toledo & Hernández, 1979). These passerine-pollinated *Erythrina* species are presumed to represent an ancestral condition with respect to the hummingbird-pollinated groups including sect. *Erythrina*. Orioles and other icterids are known to behave as nectar robbers, in a similar manner to their behavior at *Erythrina*, at other plant species in the Neotropics, including banana (*Musa paradisiaca*), which was introduced from the Old World tropics (Skutch, 1954). In the case of *Erythrina*, the evolutionary relationship of the orioles' nectar-robbing behavior of the hummingbird-pollinated species to their legitimate pollination of the putatively ancestral passerine-pollinated species remains an open question. Did orioles switch to nectar-robbing after having evolved nectar-feeding behavior as legitimate pollinators, or was the order reversed?

Several species of the honeycreeper family (Coerebidae) are nectar robbers of *Erythrina* flowers. I observed the flower-piercer *Diglossa baritula* robbing *E. chiapasana* in the highlands of southern Mexico by holding the corolla with its specialized hooked upper mandible and piercing it with its lower mandible to extract the nectar. Hernández and Toledo (1979) observed similar behavior by the same bird species at *Erythrina leptorhiza*, an herbaceous species of highland central Mexico.

Two coerebid bird species, the shining honeycreeper *Cyanerpes lucidus* and the bananaquit *Coereba flaveola*, were nectar robbers of *Erythrina tuxtlana*. These birds sometimes pierced calyces in the manner of *Diglossa*, and at other times slipped their bills into the calyx mouth without puncturing it, in the manner of the short-billed hummingbird nectar thieves. Like the orioles, these two honeycreepers that behave as robbers of hummingbird-pollinated *Erythrina* species are also important legitimate pollinators of passerine-pollinated *Erythrina* including *E. poeppigiana* in Trinidad (Feinsinger et al., 1979) and *E. megistophylla* in Ecuador (Steiner, 1979).

The migrant rose-breasted grosbeak *Pheucticus ludovicianus* (Fringillidae) nectar-robbed a living fencepost row of hybrid *Erythrina berteriana* × *E. folkersii* and natural populations of *E. folkersii* and *E. tuxtlana*, all on the Atlantic slope of Chiapas, Mexico. Unlike the other pas-

TABLE 3. Daily nectar production in flowers of *Erythrina* sect. *Erythrina*.

| Species (Locality) | Nectar Volume \bar{x} μ l \pm s.d. | \bar{x} Sucrose Equivalence Wt/Vol | \bar{x} Calories per Flower | N |
|--|---|--|----------------------------------|----|
| A. First-day flowers | | | | |
| <i>E. costaricensis</i> (San Vito de Java) | 36.4 \pm 14.7 | 29% | 43.8 | 10 |
| <i>E. globocalyx</i> (Las Nubes) | 31.4 \pm 19.5 | 22.8% | 29.3 | 10 |
| <i>E. chiapasana</i> (El Sumidero) | 29.6 \pm 12.0 | 27.3% \pm 3.9% | 33.3 | 12 |
| <i>E. goldmanii</i> (El Sumidero) | 31.9 \pm 14.6 | 28.9% \pm 2.2% | 38.2 | 10 |
| B. Two-day accumulation of nectar | | | | |
| <i>E. chiapasana</i> (El Sumidero) | 49.8 \pm 26.1 | 27.3 | 56.0 | 6 |
| | Estimated caloric production of second-day flower (B-A): | | 22.7 | |
| <i>E. goldmanii</i> (El Sumidero) | 52.3 \pm 14.1 | 31.1 | 68.1 | 9 |
| | Estimated caloric production of second-day flower (B-A): | | 29.9 | |

serine robbers, grosbeaks actually consumed floral tissue as well as nectar. Usually they plucked the flower and either crushed the calyx with their bills and dropped the flower or consumed the entire flower. At times grosbeaks merely bit off the end of the corolla (and pistil), leaving the flower attached with the calyx and corolla stump. On several occasions I observed the short-billed hummingbird *Amazilia tzacatl* follow a foraging grosbeak and insert its bill into the decapitated *Erythrina* corolla tube to extract the remaining nectar.

On a number of occasions I observed parrots (Psittacidae) consume immature seeds of *Erythrina* trees, but never the flowers. Skutch (1971), however, reported the orange-chinned parakeet *Brotogeris jugularis* to be an important nectar robber of *Erythrina berteriana* in southern Costa Rica. The parakeets plucked the flowers with their bill or feet, bit through the calyx to extract the nectar, and dropped the flowers without consuming floral tissue.

NECTAR PRODUCTION AND CALORIC VALUE

Daily nectar production per flower in the sampled populations of *Erythrina chiapasana*, *E. costaricensis*, *E. globocalyx* and *E. goldmanii* is shown in Table 3. Within populations, the variance in nectar production per flower was high (for example, the range in *E. globocalyx* was 10–67 μ l). The mean nectar volume for each of the four populations (30–36 μ l) was quite similar, however. The sugar concentration of the nectar

varied relatively little within or among populations (23%–29%). The calculated mean caloric value of the nectar per flower ranged from 29 to 43 cal among the sampled populations, with an overall mean of 36 cal.

Nectar continued to accumulate on the second day of flowering in the bagged flowers of *E. chiapasana* and *E. goldmanii*. The estimated caloric production of the second-day flowers (overall mean = 27 cal) was somewhat less than in the first-day flowers, but this may have been due to inhibition of production by the accumulation of large nectar volumes in the protected flowers, in the absence of removal by nectarivores.

The results of the nectar sampling from the different species were similar enough to allow a rough estimate of the daily caloric production per flower for hummingbird-pollinated sect. *Erythrina* in general. For purposes of the discussion below, an average caloric production of 35 cal per flower per day is assumed as an approximation. This is somewhat less than the values reported by Stiles (1975) for hermit-pollinated *Heliconia* species (48–141 cal) but is an order of magnitude or greater than the production typical of plants pollinated by short-billed generalist hummingbirds (Feinsinger, 1978).

HUMMINGBIRD ENERGETICS AND NECTAR REWARDS

Macmillen and Carpenter (1977) derived a regression equation for the 24-hour energy costs of nectar-feeding birds, based on empirical data on basal metabolic rates and energetic costs of

flight for hummingbirds, Hawaiian honeycreepers, and African sunbirds. Using this equation, the daily energetic cost for a *Heliomaster* weighing 8.0 g is calculated to be 10.9 kcal. This is the equivalent of 311 *Erythrina* flowers at 35 cal/flower. (Hummingbirds do gain some nourishment by consuming arthropods, so the actual daily nectar consumption of an *Erythrina* pollinator may be somewhat less.)

Erythrina species in sect. *Erythrina*—even large canopy trees at the peak of their blooming period—do not generally produce as many as 300 flowers per day. Therefore an individual is probably not “worth” defending as a feeding territory by a hummingbird; several trees must be visited daily to satisfy the bird’s energetic requirements.

Intertree movement of the foraging birds, and consequent pollen flow between trees, is evidently promoted by the limited number of flowers produced on an individual tree. In contrast, the extended blooming period of *Erythrina* and the predictability of the nectar resource promotes the high fidelity of visitation exhibited by the traplining pollinators. This syndrome is exemplified by my data on flowering behavior and pollination observations of populations of several different species of *Erythrina*, discussed below.

Erythrina cochleata. *Erythrina cochleata* is a 25-m tall canopy tree at La Selva Biological Station, a tropical wet forest site in Costa Rica. I attempted to locate every reproductively mature individual of this species in an area of about 2 km² at La Selva and found a total of 10 trees. This species is confined to the alluvial terraces of the rivers and major streams, so on a large scale the trees were clumped, but no individual was less than 50 m from its nearest conspecific neighbor. *Erythrina cochleata* flowers during the wet season, and the population was in flower continuously at least from May through September 1981.

I observed flower production and floral visitors for six days at four different individual trees. The trees averaged 112.5 (range 84–181) open flowers per day. The pattern of floral visitation each day was very consistent. The only pollinator and regular visitor was *Heliomaster longirostris*. Each morning between 7:00 A.M. and 8:30 A.M. a solitary *Heliomaster* would arrive, visit as few as four to as many as 45 *Erythrina* flowers, and depart. These visits were repeated at sporadic intervals during the morning. (Birds were not

tagged, so subsequent visits may have been made by different individual birds.)

On only two occasions was more than one hummingbird seen at a time in an *Erythrina cochleata* crown, and both times the interloper (once another *Heliomaster*, once a nectar-thieving *Chalybura urochrysis*) was chased away by the *Heliomaster*.

Heliomaster longirostris is considered an “uncommon” bird at La Selva (Slud, 1960), yet I saw this species every time I looked for it at flowering *Erythrina* trees. Evidently the small, scattered population of *Erythrina cochleata* supports the nutritional requirements of, and receives consistent pollination service from, a small population of *Heliomaster* for a period of several months each year. What the *Heliomaster* hummingbirds do when the trees cease flowering is unknown. They may migrate to populations of other *Erythrina* species on the Atlantic slope of Costa Rica, such as *E. steyermarkii*, that flower during the dry season, or they may forage at other canopy flowers such as *Mandevilla* spp. vines (besides *Erythrina*, there are no other hummingbird-pollinated canopy-level trees in the region).

Erythrina goldmanii. The habitat and population structure of *Erythrina goldmanii* at Cañon del Sumidero National Park in Chiapas, Mexico, where I observed this species, are very different from those of *E. cochleata* at La Selva, but the pollination systems of the two species are quite similar.

Erythrina goldmanii is a dry forest species and is rather scrubby, rarely attaining a height of over 6 m. At El Sumidero, on a slope above the semi-arid basin of the Rio Grijalva, *E. goldmanii* forms dense populations of small trees in disturbed secondary forest. I made observations in a 2 ha plot containing 54 plants. Most trees had only one or two inflorescences in bloom, with less than 10 flowers per tree; the largest tree had 36 flowers. In all there were 475 flowers in the 2 ha plot at peak flowering.

Heliomaster constantii was the only pollinator and the only hummingbird visitor seen at *Erythrina goldmanii* in over 45 hours of observation. At least three *Heliomaster* individuals were regularly in the area, with considerable movement between *Erythrina* plants, and I frequently watched them forage up and down the slope well beyond the boundaries of the plot. Their fidelity to *Erythrina* was very high: only twice did I see

a *Heliomaster* visit any other plant, and then only for single floral probes.

Orioles were frequent visitors to *Erythrina goldmanii*, and they destroyed an estimated 21% of the flowers daily in the manner described previously. There may have been competition for nectar resources between the orioles and the *Heliomasters*, but I never observed any aggressive interactions between orioles and hummingbirds.

Species of *Erythrina* sect. *Erythrina* are usually allopatric, being separated by elevation and habitat; but at El Sumidero two species come into contact. *Erythrina goldmanii* inhabits the dry lower slopes at about 800 m, and *E. chiapasana* occurs in the moister forest on top of the plateau at 1,100 m. *Heliomaster constantii* visited *Erythrina chiapasana* just as it did *E. goldmanii* less than a kilometer away downslope. Both *Erythrina* species and spontaneous hybrids were found in the intermediate zone, on the upper slopes of the El Sumidero escarpment (Neill, in press). The birds evidently do not discriminate among *Erythrina* species when the species occur together. *Heliomaster* hummingbirds are certainly the pollen vectors implicated in interspecific gene flow between *Erythrina* species at El Sumidero.

Erythrina tuxtlana. One final observation indicates that traplining hummingbirds will sometimes behave as facultative territorialists if they are given the opportunity. I observed floral visitors to a 20 m tall *Erythrina tuxtlana* in mid-elevation wet forest near Malpasó, Chiapas. The tree had a broad-spreading crown with 1,400 open flowers. According to the estimates of nectar production in other species, this should have been enough to support several hummingbirds. In fact, three hummingbirds of three different species (*Heliomaster longirostris*, *Eugenes fulgens*, and *Anthracothorax prevostii*) partitioned the crown of the tree into feeding territories and maintained the territories throughout the morning. When not feeding, each bird generally perched within its territory, and many aggressive interactions ensued when one bird crossed into another's territory. This was the only instance of consistent within-tree territoriality I observed in any *Erythrina* population.

CONCLUSIONS: IS IT COEVOLUTION?

The flowers of *Erythrina* sect. *Erythrina* provide a rich nectar resource that is fed upon by many species of birds besides the legitimate pol-

linators. The pollinators, however, constitute a small guild of "high-reward traplining" hummingbirds, about eight species in Mesoamerica. These are mostly non-hermits of the subfamily Trochilinae. Predominant among these is the genus *Heliomaster*. The pollinators are highly faithful visitors to *Erythrina*, which provides them with a consistent nectar resource for long periods. The limited caloric value of nectar produced per tree per day usually precludes the maintenance of permanent feeding territories at a single tree by the hummingbird visitors. The consequent nomadic or "traplining" behavior of the hummingbirds and the dispersal patterns of the pollen they transport among the scattered individual *Erythrina* trees may be a critical factor in the mating systems and genetic structure of the low-density *Erythrina* populations.

The pollination system of sect. *Erythrina*, in summary, is a canopy-level analogue of the high-reward traplining pollination systems of *Heliconia* and similar understory plants. In this sense the pollination system of sect. *Erythrina*, together with the other hummingbird-pollinated sections of *Erythrina* trees (sects. *Stenotropis*, *Pseudo-edules*, *Gibbosae*, and *Corallo dendra*; cf. Neill, in press) may be unique. Hummingbird-pollinated canopy and subcanopy trees are in themselves uncommon (Stiles, 1978), and I know of no other genus of canopy trees besides *Erythrina* that is adapted to pollination by the traplining guild of hummingbirds.

To what extent have species of sect. *Erythrina* and their hummingbird pollinators coevolved? To what extent is this a specialized mutualism? Feinsinger (1983) indicated that a highly specialized, one-to-one relationship between hermit hummingbirds and their food plants is a rare occurrence; although they may specialize on a particular plant species temporarily, most hermit species forage on a number of different plants. Similarly, most hermit-pollinated plants are serviced by several species of hermits, although shorter-billed birds are excluded as pollen vectors. If one's definition of coevolution requires a high degree of one-to-one species specificity in such mutualistic interactions, then hermits and hermit-pollinated plants cannot be considered very "tightly coevolved." Feinsinger (1983) considered that "most hermits, hermit-like hummingbirds and their food plants exemplify diffuse coevolution between two diverse groups of species."

Species of sect. *Erythrina* vary in the degree of specificity of their association with the hummingbird pollinators. *Erythrina* species of the dry forests of the Pacific slope are pollinated exclusively by *Heliomaster constantii*, so the plant's fitness is directly dependent on the behavior and morphology of a single bird species. The opportunity for the plant to evolve adaptations to specific traits of the bird is clear. *Heliomaster constantii*, however, feeds upon and pollinates a number of *Erythrina* species throughout the bird's geographic range, and it also feeds upon and pollinates at least one other plant genus (*Mandevilla*; Feinsinger, pers. comm.). Although there is undoubtedly a temporary sort of exclusivity in the *Erythrina*-*Heliomaster* association in certain ecological communities at certain seasons of the year, the association cannot really be considered an obligate mutualism.

The plant-pollinator association is less specific for *Erythrina* species of highland and wet-forest communities, where several species of traplining hummingbirds often visit and pollinate an individual tree on a single day. Hummingbirds such as *Eugenes* and *Campylopterus* visit a rather wide variety of plants besides *Erythrina*. Even in these cases, however, such plant-pollinator associations involving high-reward traplining hummingbirds are much more exclusive than those involving short-billed generalist hummingbirds and short-corolla plants.

Among the species of sect. *Erythrina*, there is little differentiation in floral morphology, flowering patterns, or morphology and behavior of the pollinators—the pollination system of all species is quite similar. Rather, species are differentiated by their restriction to distinct climatic and edaphic conditions. This large group of species, as a whole, has evolved a particular set of adaptations to the guild of high-reward traplining hummingbirds.

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APPENDIX

Locality and Voucher Data for *Erythrina*
Populations Used in Observations of Floral Visitors
(Numbers correspond to those listed in Table 1)

1. *E. americana* Miller. Mexico: Oaxaca, 5 km E of San Pablo Coatlan. 16°12'N; 96°47'W. Elev. 1,450 m. Disturbed gallery forest with *Taxodium*, and cultivated fields. Tree to 20 m, along intermittent stream. 9–10 Feb. 1983. *Neill* 5421, 5424.
2. *E. berteroana* Urban × *E. folkersii* Krukoff & Moldenke. Mexico: Chiapas, 3 km S of Palenque. Elev. 100 m. 17°28'N; 92°00'W. Fencepost bordering field. Tree to 8 m. 18 March 1983. *Neill* 5533.
3. *E. berenices* Krukoff & Barneby. Mexico: Veracruz, Tequila. 19°45'N; 97°03'W. Elev. 1,650 m. Coffee plantation; Premontane Wet Forest. Tree to 12 m. 26 Jan. 1983. *Neill* 5381.
4. *E. chiapasana* Krukoff. Mexico: Chiapas, El Sumidero National Park, Km 14–16. Elev. 1,100 m. 16°47'N; 93°06'W. Disturbed Premontane Dry Forest, transition to moist mixed *Quercus* forest. Tree 15 m. 2–4, 9, 25 March 1983. *Neill* 5455, 5458, 5465.
5. *E. chiapasana* Krukoff. Mexico: Chiapas, 13 km E of Teopisca. Elev. 2,000 m. 16°30'N; 92°25'W. Pine-oak forest. Tree 7 m. 22–23 March 1983. *Neill* 5445.
6. *E. cochleata* Standley. Costa Rica: Heredia, La Selva Biological Station. Elev. 200 m. 10°24'N; 84°00'W. Tropical Wet Forest. Tree 25 m. 15–18 Aug., 18–21 Sept. 1981. *Neill* 5015, 5101.
7. *E. costaricensis* Micheli. Costa Rica: Puntarenas, San Vito de Java, Las Cruces Botanical Garden. Elev. 1,200 m. 8°45'N; 82°55'W. Premontane Rain Forest, roadside. Tree 6 m. 11–12 Sept. 1981. *Neill* 5099.
8. *E. gibbosa* Cufodontis. Costa Rica: Alajuela, upper Penas Blancas Valley, below Monteverde Reserve. Elev. 1,400 m. 10°20'N; 84°45'W. Premontane Rain Forest; edge of pasture. Tree to 4 m. 4–6 Sept. 1981. *Neill* 5057.
9. *E. globocalyx* Porsch & Cufodontis. Costa Rica: San Jose, Las Nubes. Elev. 1,700 m. 9°53'N; 24°00'W. Fencepost row, border of pasture. Tree to 8 m; sporadic along stream. 14 Aug., 25 Sept. 1981. *Neill* 5033, 5142.
10. *E. goldmanii* Standley. Mexico: Chiapas, El Sumidero National Park, Km 7. Elev. 900 m. 16°47'N; 93°06'W. Tropical Dry Forest; secondary, disturbed scrub. Tree 8 m. 25 Feb.–1 March 1983. *Neill*, 5497, 5498.
11. *E. folkersii* Krukoff & Moldenke. Mexico: Veracruz, Los Tuxtlas Biological Station. Elev. 200 m. 18°31'N; 95°03'W. Tropical Wet Forest. Understory/subcanopy tree to 8 m. 28 Jan. 1983. *A. Gentry* 32490.
12. *E. folkersii* Krukoff & Moldenke. Mexico: Chiapas, Palenque Archaeological Site. 17°29'N; 92°01'W. Tropical Wet Forest; forest edge. Tree 5 m. 19 March 1983. *Neill* 5534.
13. *E. lanata* Rose. Mexico: Oaxaca, 37 km W of Puerto Escondido. Elev. 20 m. 15°90'N; 97°20'W. Tropical Dry Forest, scrub. Tree 6 m. 13 Feb. 1983. *Neill* 5430.
14. *E. lanata* Rose. Mexico: Jalisco, Chamela Biological Station. Elev. 250 m. 19°30'N; 105°03'W. Tree 7 m. 13 Jan. 1983. *Neill* 5329.
15. *E. pudica* Krukoff & Barneby. Mexico: Chiapas, Rio de la Venta, Cascada El Aguacero. Elev. 750 m. 16°46'N; 93°33'W. Tropical Dry Forest, scrub. Tree 6 m. 27, 31 March 1983. *Neill* 5512.
16. *E. tuxtiana* Krukoff & Barneby. Mexico: Chiapas, 25 km N of Ocozocuahtla. Elev. 700 m. 16°48'N; 93°25'W. Premontane Wet Forest; karst limestone. Tree to 20 m. 28 March, 9 April 1983. *Neill* 5486, 5621.
17. *E. tuxtiana* Krukoff & Barneby. Mexico: Veracruz, Uxpanapa. Elev. 90 m. 17°11'N; 94°39'W. Tropical Wet Forest; karst limestone. Tree 15 m. 16–17 April 1983. *Neill* 5642.